

Planktonic Larval Duration, Age and Growth of *Ostorhinchus doederleini* (Pisces: Apogonidae) on the Southern Great Barrier Reef, Australia

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Keywords: Apogonidae, otoliths, age, PLD, settlement, growth, mortality.

25

26 **Abstract**

27 Cardinalfishes (Apogonidae) are abundant on corals reefs, but there are few data on demography to
28 understand trophodynamics and population dynamics. *Ostorhinchus doederleini* is a small and abundant
29 apogonid on the Great Barrier Reef (GBR) and throughout the Western Pacific Ocean. We present key
30 demographic parameters for the entire life history from the southern GBR. Daily deposition of
31 increments in otoliths was validated. Fish had a Planktonic Larval Duration (PLD) of 16 to 26 days.
32 PLD was established from fish collected immediately prior to settlement as no settlement mark was
33 found. Fish grew at about 0.35 mm d^{-1} for the first 20 d after settlement. Fish reached a maximum
34 standard length at about 200 d and no fish lived longer than 368 d at four reefs separated by kilometers
35 to tens of kilometres. There was no evidence for differences in size at age between sexes. Mortality
36 was very high, for fish greater than 60 days old mortality rates ranged from 2.9 to 4.6% per day. Short
37 lives and high mortality rates makes *O. doederleini*, and potentially other apogonids, vulnerable to
38 recruitment failure. Here we review data on the demographic characteristics of other reef fishes.
39 Although some taxa live to over 50 years, the short lives of apogonids are most aligned with the
40 Gobiidae and Blenniidae (i.e. typically < 1.5 years). Descriptions of fish size, age, longevity, growth
41 and mortality; from hatching to age maxima are very rare for most taxa, even at the level of family.

42

43 **Introduction**

44 Nocturnal fishes are an important trophic group on both coral and temperate reefs (e.g. Marnane and
45 Bellwood 2002; Annesse and Kingsford 2005). Fishes belonging to the Apogonidae, Holocentridae,
46 Nemipteridae and Pempheridae are abundant on reefs and species richness is high (Hobson and Chess
47 1978; Sale and Douglas 1984; Bellwood 1996; Greenfield 2003; Mabuchi et al. 2006; Thacker and Roje

2009; Gardiner and Jones 2010; Boaden and Kingsford 2012). These taxa feed at night on a range of invertebrates and fishes (Hiatt and Strasberg 1960; Marnane and Bellwood 2002; Annesse and Kingsford 2005; Barnett et al. 2006) and are the prey of many piscivorous taxa (e.g. Kingsford 1992).

Apogonids, and other nocturnal fishes, generally occupy caves and other habitats that provide shelter (e.g. coral Gardiner and Jones 2005) during the day and undergo feeding migrations at night. Movements range from spatial scales of metres to hundreds of metres. In general these fishes feed in habitats that are different from those they occupy during the day (Gladfelter 1979; Marnane 2000; Annesse and Kingsford 2005; Boaden and Kingsford 2012). The trophic importance of these movements to reef ecosystems ~~are-is~~ potentially substantial in that their feeding behavior and availability to predators are likely to be significant carbon pathways. Furthermore, feeding behavior often varies with size of fish. Many apogonids and other young nocturnal fishes (Annesse and Kingsford 2005) feed in different habitats than large juveniles and adults (Finn and Kingsford 1996).

Most apogonids have paternal mouth brooding and a larval phase (Brothers et al. 1983). An exception, the apogonid *Pterapogon kauderni* has paternal mouth brooding and direct development of juveniles with no larval phase (Vagelli and Volpedo 2004). Great attention has been given to filial cannibalism of eggs brooded in the buccal cavity of males *O. doederleini* (Okuda and Yanagisawa 1996) and other species (Okuda et al. 1997; 2003; Kume et al. 2000). Despite their novel reproductive biology, trophic importance and the recognition that there is high local population turnover (e.g. on patch reefs Sale and Douglas 1984), there are few data on demography (but see Okuda et al. 1998). An exception is Longenecker and Langston (2006) who found that *Ostorhinchus rubrimacula* (Apogonidae) lived to a maximum of 274 days at a reef in Fiji. There are some estimates of Planktonic Larval Duration (PLD) for 14 species of apogonids in Japan (mean PLDs ranged from 14 to 31 days, Ishihara and Tachihara 2011), but the generality of these values is unknown.

A thorough understanding of population dynamics of any species requires information on growth and mortality at all stages of life history (Hilborn and Walters 1992). The potential for high volatility in population size would be greatest in species that have low age-maxima as there would be little in the way of ‘stored’ year classes from seasons of high recruitment. Great variation in coral reef fish recruitment among seasons is common (Doherty and Williams 1988), but populations persist, often supported by a small number of large peaks in recruitment (Doherty and Fowler 1994; Kingsford 2009). Apogonids are abundant on tropical reefs, but predation on these fishes is known to be very high (e.g. Sale and Ferrell 1984). We have not found any other studies on the growth of apogonids prior to settlement, immediately after settlement and to their age maxima. We hypothesised that age maxima in *Ostorhinchus doederleini* would be low and this would be consistent among reefs. If this were the case it would greatly influence the outcomes of connectivity among reefs and the persistence of population genotypes. Recent evidence suggests that reef-based local populations of *O. doederleini* can be genetically distinct even when the reefs are only separated by kilometers to tens of kilometers. It has been proposed that despite the relatively poor swimming abilities of larval apogonids (Stobutzki and Bellwood 1997), they are capable of detecting olfactory cues from their natal reefs and this combined with larval behavior facilitates reduced dispersal that can create genetically distinct populations (Gerlach et al. 2007), but a knowledge of fish demography is essential for a full understanding of connectivity.

The objective of the present study was to describe the growth and mortality of *Ostorhinchus doederleini* (Jordan and Snyder 1901) at four sites within the southern Great Barrier Reef. We examined otolith microstructures to (1) validate the aging technique, and (2) determine the Planktonic Larval Duration (PLD), the duration of the presettlement phase. We also, (3) describe the early growth characteristics in presettlement and newly settled fish and (4) potential differences in the growth rates and demographics of fish at multiple reefs. We also provide information on (5) mortality rates based

upon length-at-age estimates of post-settlement fishes. Finally, we (6) review and compare the demographic characteristics of apogonids with other reef fishes.

Materials and methods

Study sites and fish sampling

Ostorhinchus doederleini were sampled at multiple sites on four reefs of the Capricorn Bunker group, southern Great Barrier Reef: Heron Island, One Tree Island, Lamont and Fitzroy reefs (Fig. 1). Presettlement fish were only collected at One Tree Island. Channel nets were set to sample fish on the flood tides only at night in January 1994, February 1995 and February 2009 (Table 1). The net was square mouthed (0.75 x 0.75 m), the mesh was 500 μ m, organized as a box/pyramid with an efficiency of 1:12 (mouth area: open sifting surface; full procedures see Kingsford and Finn 1997). To preserve the calcium carbonate of otoliths, subsamples of collections from nets were preserved in ethanol. Samples were then rinsed in alcohol to reduce the seawater content, the final percentage ethanol was 80%. *Ostorhinchus doederleini* entering the lagoon to settle were easily identified by morphology and pigmentation (e.g. a black dot on the caudal peduncle).

Newly settled *O. doederleini* (10 to 18 mm SL) settle on sand and often away from continuous reef (Finn and Kingsford 1996). We constructed six peaked patch reefs on sand (diameter ~ 1.5 m by 0.5 m maximum height) 20 to 60 m from continuous reef. Patch reefs were monitored on a daily basis and all newly settled fish were collected with fine-meshed hand nets and a wide size range was preserved in 80% ethanol for ageing. Some fish that colonized patch reefs were larger than new settlers (18 to 27 mm SL), but were collected for a description of early post-settlement growth (Table 1).

Juvenile and adult *O. doederleini* were collected at four reefs during January and February of 2009, 2010 and two large individuals in 2013 (Table 1). At each reef we sampled at multiple sites separated by hundreds of metres to tens of kilometers to obtain a representative sample, and fish were pooled for analyses. Juveniles and adults were collected from caves or branching coral, (especially *Porites cylindrica* and branching *Acropora* spp.) and preserved in 80% ethanol. A wide size-range of fish were collected using a mix of 5:1 ethanol: clove oil. At Heron Island and Lamont reef, we sampled all fish from some large patch reefs and this allowed us to estimate mortality rates (see below). Great care was taken to obtain all size classes of fish, especially large individuals that can be missed because they are the most secretive in the backs of caves. Because *O. doederleini* were potentially short-lived (e.g. Longenecker and Langston 2006) we also sampled fish in October 2010 in case the time of sampling altered our estimates of age maxima; these samples did not allow estimates of mortality as only large fish were selected. All fish collected in October 2010 were sexed macroscopically (ie the presence of oocytes in females or fine-grain spermatogenic tissue in males) to determine size and age versus sex relationships.

Otolith preparation

Increments in otoliths were used to obtain estimates of the age and growth of *O. doederleini*. All fish were weighed (± 0.01 g) and then measured (standard length [SL] ± 1 mm). Sagittal otolith pairs were dissected, rinsed in water, and dried overnight. One otolith from each pair was randomly selected, embedded to the edge of a glass microscope slide using Crystal Bond thermoplastic glue. The sulcal groove of the otolith was orientated perpendicular to the surface of the slide and outer edge of the primordium was flush with the inside edge of the slide. Slides were then held vertically and ground to the transverse mid-plane using a Gemmasta GF4 Faceting Machine with a 3000 μ diamond encrusted

steel disc. The glue was then reheated and otoliths were remounted with the newly ground surface placed face down in the centre of the glass slide. Otoliths were ground until a thin section (20 μm thick) was obtained which included the primordium.

Analysis of growth increments

The opaque zones visible in the internal structure of the otolith were counted along a radius from the primordium to the outer edge of the otolith from an image taken with a compound microscope (Leica DMLB using a Leica DC300 digital camera); a white incident light source was used. Alternating translucent and opaque increments were interpreted as daily rings; no annuli were observed, even in the largest fish. The counting of increments began from the first clear increment closest to the primordium. Sections were coded and examined in random order and the opaque increments counted on two occasions by the same observer separated by at least seven days. Counts of daily rings were compared between these two occasions in order to assess the confidence that could be placed in the interpretation of otolith structure. If increment counts differed by more than 10% between counting occasions, then the otoliths were re-examined. If, following a third reading, agreement between the third and one of the two other counts was not reached (only closely matching counts were used in analyses), then the otolith was not included in the analysis. To calculate the age, an average of the two closest age estimates was used. Rejection rate over the entire sample was 2.8%, leaving a total sample of $n=581$ for aging.

Validation of aging technique

To determine the periodicity of increment deposition in *O. doederleini* otoliths, a validation experiment (using tetracycline) was completed at One Tree Island Research Station in January 1994. Fish were treated with tetracycline, it is transported to the endolymph of the inner ear via the blood and deposited

in the otoliths and other bony tissues as a mark (Odense and Logan 1974). The tetracycline mark can be viewed as a fluorescent line under ultraviolet light. The otoliths of 20 untreated fish were examined for autofluorescence.

Newly settled and other juvenile *O. doederleini* between 16.2 and 32.0 mm SL were collected from isolated patch reefs. Fish were collected with a small hand net and transferred to buckets filled with seawater for transport back to the laboratory. They were immersed in tetracycline-treated seawater (0.25 g L⁻¹) for 18 hours in the laboratory in order to mark their otoliths (higher concentrations killed small fish). Fish were transferred to 25 L buckets with one mm mesh windows in the lagoon after removal from the tetracycline solution. Treated fish, therefore, were exposed to the natural cycle of day and night and to normal levels of salinity and water temperature. Fish were fed on wild zooplankton and *Artemia nauplii* that were reared in the laboratory. Fish of a range of sizes were euthanased after five, 10 and 15 d; fish were then preserved in 98% ethanol. Sagittal otoliths were removed, processed and viewed under transmitted and fluorescent light using a compound microscope. Under fluorescent light an ocular marker was aligned with the fluorescent band if present. The otolith was then viewed under natural light and increments counted between the ocular marker and the otolith margin. Processed otoliths from a similar size range of untreated *O. doederleini* were also examined for the presence of auto fluorescence. All otoliths were examined without knowledge of size or treatment.

Spacing of otolith increments

Most reef fish have a mark in otoliths that corresponds with the time of settlement (Brothers et al. 1983). Settlement marks are an abrupt change in increment spacing, usually from wide to narrow (Victor 1986; Kingsford et al. 2011). Our initial observation of otoliths in recently settled fish failed to detect a settlement mark. We tested this more critically by measuring the spacing of increments in eight

randomly selected juvenile *O. doederleini* to determine how the increment pattern changed with distance from the primordium. Transverse sections of the sagittal otolith were prepared. In the first group of fish increment widths were measured from the primordium to the otolith margin (n = 4 fish) and in the second group of fish, from sulcal groove along the longest axis of the otolith to the ventral edge (n = 4 fish) were measured. Increment widths were measured using a calibrated video-analysis system (Leica IM50) linked to a compound microscope (Leica DMLB).

Age and Growth

Growth was described using the von Bertalanffy growth function (VBGF) which provided the best fit to size-at-age data when compared with estimates of the Schnute growth function (Schnute 1981). The von Bertalanffy expression for length at age t (L_t), as a function of time was calculated using equation (1):

$$L_t = L_{\infty} [1 - e^{-K(t-t_0)}] \quad (1)$$

where L_t = length at age t (days), L_{∞} = the mean asymptotic standard length, K = the rate at which the growth curve approaches L_{∞} , and t_0 = the age at which the fish have a theoretical length of zero. The growth function was run by solver (Microsoft Excel) which minimizes the sum of squares by changing L_{∞} , K and t_0 . Some of our demographic comparisons use ‘Age max’ = maximum age of an individual within a sample; and adapted from the convention of Choat and Robertson (2002), max 5% refers to the average age of fish from the 95th to 100th percentile, max 10% the average age from the 90th to the 100th percentile of the sample.

Mortality

The instantaneous rate of mortality (Z) was calculated using log-linear regression analyses of age-frequency data sets for *O. doederleini* populations from two reefs where all fish from new recruits to large adults were collected. This method assumes that recruitment is consistent over time at each reef (Haddon 2001). Year classes to the left of the age-frequency mode were excluded from the analysis because our sampling technique was biased against small fish. Mortality was only estimated where fish (over 45 mm SL) were collected representatively (i.e. Heron Island and Lamont reef). The slope of the regression line for each reef provided an estimate of daily instantaneous mortality (Z); equation (2), when expressed as a percentage = loss of individuals per day.

$$Z = F + M \quad (2)$$

where F is fishing mortality and M is natural mortality (Gust et al. 2002). Since there is not a fishery for *O. doederleini* on the GBR, F equals zero and therefore Z estimates natural mortality only. Daily survival rate estimates (S) were then calculated (i.e. percentage surviving per day, Ricker 1975) according to the equation (3).

$$S = e^{-Z} \quad (3)$$

Data from each site were pooled for each reef. Similarities in mortality rates among replicate reefs allowed comparisons of mortality between reefs.

Results

Validation of aging

The otoliths of most *Ostorhinchus doederleini* (75%) immersed in tetracycline showed a bright fluorescent band close to the otolith edge (Fig. 2b). Twenty untreated *O. doederleini* otoliths were checked for autofluorescence and showed no fluorescent band ($n = 20$). There was close agreement between the number of increments laid down from the time of immersion in tetracycline and known number of days since treatment; this was true of fish sampled at 5, 10 and 15 days (Table 2).

Settlement marks were not found in *O. doederleini* regardless of the orientation of counts with respect to the otolith primordium (Fig. 3a & c). There were no rapid changes in increment width that could be attributed to settlement. The approximate age at settlement could be estimated from the average age that potential settlers entered the lagoon to settle (Fig. 3a & b, Table 3). Although increment width varied across the otolith, they did not relate to settlement. Increments close to the primordium ranged from 2 to 4 μm in width and at approximately the 5 to 8 day mark increments rapidly became wider (5 to 7 μm); Fig. 3a. The rapid increase in increment widths at the 5 to 8 day mark was not related to settlement as the mean number of increments in *O. doederleini* caught just prior to settlement was 19.5 (SE = 0.38, $n = 34$; Table 3). Similar patterns were found in separate profiles, but increments were generally wider (5 to 18 μm) across the profile (Fig. 3b).

Age and size of presettlement and recently settled *Ostorhinchus doederleini*

The age of presettlement *O. doederleini* caught in the channel nets ranged from 15.7 to 26.0 days (mean = 19.9; $n = 34$) and SL ranged from 7.5 to 13.8 mm (mean 10.7; $n = 34$); Table 3. The age of recently settled *O. doederleini* collected from experimental patch reefs ranged from 16 to 42 days (mean = 25.0; $n = 232$) and SL ranged from 8.6 – 18.0 mm (mean 12.7; $n = 677$); Table 3.

There was great overlap in the age and size of presettlement fish entering the lagoon and that of recently settled fish. Youngest fish on patch reefs were 16 to 17 days old and were as small as 8.6 mm SL. Older and larger fish were found on patch reefs, but many of them would have been associated with the reef for days as some recently settled fish move between patch reefs (Finn and Kingsford 1996). There was a strong linear relationship between age and standard length in presettlement fish over the first 20 days and recently settled fish and growth was rapid at about 0.35-26 mm per day (Fig. 4).

Variation in growth and sizes among reefs

The maximum age of *O. doederleini* among all reefs was 368 days ~~old~~ and at most reefs few fish were older than 200 days old (Fig. 5; Table 4). Time of sampling did not affect estimates of age maxima. The oldest fish caught in January to February at One Tree Island was 284 days and 59 mm long (SL), while in October it was 263 days and 62 mm long (SL). When the average age of the top 5 and 10% of fish was considered at each reef, fish were 150-250 days old (Table 4). All von Bertalanffy relationships were well anchored with small fish around 15 to 20 mm SL. Best estimates of asymptotic length were obtained from One Tree Island, where fish grew little in length from 150 to 200 days old. Although there were no significant differences in the size of fish among reefs in the age range of 90 to 110 days (ANOVA, $F_{(3, 60)} = 0.568$, $P = 0.63$), the maximum size of fish did vary. By reef the average size for the top 5% of fish and the maximum SL was (average, max): One Tree Island (61.0, 66 mm), Heron (57.0, 65 mm); Lamont (62.6, 74 mm) and Fitzroy (65.5, 68 mm). The largest fish caught at Heron Island, One Tree Island and Fitzroy reef were 65 to 70 mm SL (= ~80 to 85 Total Length). The two largest and oldest fish ever collected (days/SL, mm: 246/69, 368/74) were from Lamont reef, January 2013. The mean and range of lengths (SL) and ages differed little between males and females (Table 5).

271 Mortality

272 Instantaneous mortality rates calculated from catch-curves indicated that mortality rates were high for
273 Lamont and Fitzroy reefs (2.9 to 4.6 % per day, Fig.6). Further, mortality rates were highest at Lamont
274 where large fish were rare. Survival (S) rates ranged from 0.971 to 0.955 d⁻¹.

275 Discussion

276 *Ostorhinchus doederleini* had a short PLD and once they settled, grew fast and died young. High
277 mortality rates within days of settlement are common for reef fishes (Sale and Ferrell 1988) and low age
278 maxima have been found in other apogonids (Longenecker and Langston 2006). Our study has
279 demonstrated that *O. doederleini* has a high mortality (2.9 to 4.6% per day) and a low age-max. Ages of
280 one year or less clearly put these tropical apogonids at the lower end of the longevity spectrum for
281 tropical fishes along with the Gobiidae and Blenniidae (Table 6). Although some taxa such as gobies
282 may live for less than a year and have high mortality rates (e.g. *Eviota silligata* has an age max of 59
283 days, mortality rate 7.8% per day; Depczynski and Bellwood 2005), species from families of common
284 reef fishes such as the Pomacentridae (e.g. Doherty and Fowler 1994; Kingsford and Hughes 2005),
285 Labridae (Choat et al. 2006), Scaridae (Choat et al. 1996; Gust et al. 2002), Serranidae, Lutjanidae
286 (Kingsford 2009) and Acanthuridae (Choat and Axe 1996) live for years and sometimes decades
287 (Munday and Jones 1998; Fowler 2009) Table 6. Fishes with the lowest age-max were generally small
288 and represented three different trophic groups: nocturnal planktivores, micro/meso carnivores and
289 herbivores/detrital feeders. Although short-lived reef fish appear to be small, not all small fish are short
290 lived (e.g. *Pomacentrus mollucensis* SL max 90 mm (TL) and age max 18 years; Doherty and Fowler
291 1994).

292 To the best of our knowledge, this is the first study to report information on the growth rates of *O.*
293 *doederleini* prior to settlement and immediately after settlement. Further, it is the first to provide data

on longevity (age maxima) of the species in the tropics..Some families had data on multiple stages of life history when multiple species were pooled (e.g. omnivorous/herbivorous damselfishes), but given the differences in demographic characteristics within a family general patterns would be crude or simply inaccurate. There was an abundance of data on age, growth and mortality of representatives of families that are the focus of fisheries, especially macrocarnivores and piscivores such as lutjanids, serranids and carangids. However, data on presettlement growth, PLDs and post-settlement growth was comparatively rare. In other families the focus has only, or primarily, been on early life history stages (e.g. Holocentridae, Pomacentridae). For many important families, we found no data at all on age and growth (e.g. Holocentridae, Pempheridae, Caesionidae and Pomacanthidae). The paucity of data is due in part to a relatively recent understanding that the otoliths of tropical species can provide reliable estimates of age (Meekan et al. 2001). Despite this there is a clear need to increase knowledge in this area for the management reef assemblages and tropical fisheries

We concluded that accurate estimates of age could be obtained from daily increments. Evidence that counts were accurate included the following: the technique was validated, daily increments were easily observed (Fig. 2), the asymptote for age/length relationship for all reefs was beyond 200 days and, adult fish were collected from a size of 49 mm and 132 days or older (based on brooding fish and macroscopic examination of gonads).

The oldest fish we found was 368 days (n=581); at 23°35' S) and, unpublished data by Michael Marnane at One Tree Island also indicated that some *O. doederleini* can reach an age of over one year. Similar to our study, Longenecker and Langston (2006) found that *Ostorhinchus rubrimacula* (Apogonidae) lived to a maximum of 280 days in Fiji (17°15' S). However, there are great differences

between our results for *O. doederleini*, and other data from temperate waters in Japan. Okuda et al. (1998) concluded age estimates of up to seven years in at Shikoku Island, Japan (33° 40" N). The fish sampled in Japan grew to a maximum SL of 86 mm SL whereas we only found fish to a size of 74 mm (93 mm TL). The maximum size of *O. doederleini* recorded for the GBR is 90 mm TL ~ 74 mm SL, but no location is given by Randall et al. (1990) for this specimen. Okuda et al. (1998) had few data on fish less than one year for us to make comparisons of age versus a fish of known size. There are three possibilities to explain latitudinal variation in *O. doederleini* age and growth: (1) there are great differences in age over 10 degrees of latitude, which is partly reflected by differences in size max; (2) a methodological issue where the accuracy of aging techniques varies; Okuda et al. (1998) used scales, whereas we used daily increments in otoliths; (3) mortality rates vary greatly between latitudes. With respect to options one and two, we favour option one as latitudinal variation in growth and age maxima are common in fishes (growth, Conover et al. 1997; age-max, Boehlert and Kappenman, 1980). Furthermore, scales tend to underestimate not overestimate ages. In Japan Okuda et al. (1998) fin clipped some fish that were monitored for up to two years, so they clearly get older than their tropical conspecifics. The apogonid *Apogon ruepillei* found in estuaries near Perth (~ 32°S) were over a year old (Chrystal et al. 1985). All of the evidence from tropical waters indicates that small *O. doederleini* have age maxima of a year or less. Estimates of L_{∞} would be most reliable for all reefs combined (Table 4) as very large fish were rare. Our comparisons of the size/age of fish among reefs in the 80 to 90 mm SL range would be robust, but beyond 200 days would be weak. Latitudinal gradients in growth and life span would be interesting to examine. Conover et al. (1997), for example, demonstrated a strong positive correlation between the latitude of origin of *Morone saxatilis* and growth. Further, it is common for there to be positive relationships between life-span and latitude in ectotherms, including fishes (Boehlert and Kappenman, 1980; review, Munch and Salinas 2009). At present there are no

comparative data on growth by latitude for *O. doederleini*. The presettlement phase of *O. doederleini* was 16 to 26 days and fish settled at 9.5 to 13 mm SL. Settlement marks were not observed and the age of settling fish was determined from potential settlers collected in nets at night and new arrivals to patch reefs. Ishihara and Tachihara (2011) estimated the PLDs of six *O. doederleini* in Japan at ~ 16 to 24 days and 10 to 11.5 mm SL, which fell within the ranges of values we had from the southern GBR; these authors also collected fish in channel nets. The range of ages over which fish settled was 38% of the maximum age at settlement, a little less than that recorded for the damselfish *Pomacentrus coelestis* (45%; Kingsford et al. 2011). Although many damselfishes spend a similar time in the plankton to *O. doederleini*, there are many other taxa that have longer PLDs. For example, scarids have PLDs of 34 to 58 days; chaetodonts 25 to 40 and acanthurids 80+ days (Brothers et al. 1983).

Ostorhinchus doederleini have strong olfactory senses and can respond to the presence of lagoonal waters (Atema et al. 2002). Presettlement fish swim and/or are carried over the reef crest at night (Kingsford 2001) into One Tree lagoon where they find suitable settlement habitat to settle. *Ostorhinchus doederleini* commonly settle away from continuous reef on sections of substratum, potentially to avoid predatory parents (Finn and Kingsford 1996). We demonstrated that during this phase fish had linear growth, this is typical of other fishes during the early juvenile phase (Kingsford & Milicich).

Although reef fishes often have a mark in their otoliths related to settlement from pelagic to benthic environments (Brothers et al. 1983; Kingsford et al. 2011), 'settlement marks' were absent in the otoliths of *O. doederleini*. Brothers et al. (1983) also concluded that *O. doederleini* settle at 16 to 27 days (n=5) and did not mention a settlement mark (= 'transition'). Settlement marks are not found in all fishes and, it has been speculated that the eco-behavioral transitions are less traumatic in these circumstances (e.g. monacanthids settling from drift algae to algae attached to the substratum, Kingsford

and Milicich 1987). *Ostorhinchus doederleini* may experience less post-settlement trauma by not settling on continuous reef, where the risk of predation (and stress) is high. Further, they usually settle with conspecifics (pers. obs.) and they already have an established ability to feed in low light (Job and Bellwood 2000).

There is strong evidence that population structure within a metapopulation of *O. doederleini* can be complex at spatial scales of kilometers to tens of kilometers. Despite having a PLD of 16 to 26 days, a combination of favorable oceanography and larval behavior means that a disproportionately high number of fish return to natal reefs and this can result in significant genetic differences among reefs (Gerlach et al. 2007). The robustness of population structures through time is likely to depend on larval survival, physical forcing (Sissenwine 1984), post-settlement processes (Jones 1991; Almany and Webster 2006) and demographic characteristics. It is critical to consider age for numerical modeling of ecological variation in population size and genetic robustness. For short-lived species such as *O. doederleini*, there is a great vulnerability to recruitment failure, especially if they do not have a prolonged spawning season. This in turn could compromise the resistance and resilience of a local genotype to change. Information on the timing and duration of spawning of *O. doederleini* is largely anecdotal, but does suggest a prolonged spawning season. Mouth brooding fish have been observed in October and January-February and peak recruitment is in January to February (i.e. from spawning in December and January). Further, the collection of *O. doederleini* larvae, in June by Kingsford (2001) indicates that at least some spawning occurs in winter and backdating the age of fish collected in January and February puts many birthdates in the Austral winter to spring.

In conclusion, *O. doederleini* have a short PLD, they settle onto sand and rubble away from continuous reefs and grow quickly. They reach asymptotic size beyond 200 days, but few fish reach 200 days old and the age maximum we found at four reefs was 368 days. These small fish were

386 characterized by high mortality rates and presumably have a high population turn over; this should be
387 considered in models relating to the trophodynamics of reefs and the population biology of
388 *O. doederleini*. A review of the literature indicated that other fishes with similar demographic
389 characteristics are small gobies and blennies.

390

Acknowledgements

We specifically would like to thank One Tree Island Research Station staff and Norm of the *MV Melantra* for our inter reef excursions. This project was funded by ARC Grants to MJK and funding from the ARC Centre of Excellence for Coral Reef Studies. This paper is a contribution from the Reef and Ocean Ecology Laboratory, James Cook University and One Tree Island Field Station.

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615 **Table 1** Collection details for *Ostorhinchus doederleini* specimens, 1994 to 2013. OTI- One Tree Island;
 616 H- Heron Reef; F- Fitzroy Reef; and L= Lamont.

617

| Dates Sampled | Methods used | Reefs | Life stage |
|---------------|---------------------------------------|--------------|--|
| Jan 1994 | Channel nets; Patch Reefs | OTI | Presettlement and early post-settlement |
| Feb 1995 | Channel nets; Patch Reefs | OTI | Presettlement and early post-settlement |
| Feb 2009 | Channel nets, Hand nets; clove oil | OTI, H, F, L | Juveniles and adults |
| Jan-Feb. 2010 | Hand nets; clove oil | OTI, H, F, L | Juveniles and adults |
| Oct 2010 | Hand nets; clove oil | OTI | Juveniles and adults |
| Jan 2013 | Hand nets; clove oil | L | Adults |

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621 **Table 2** Results of validation marking experiments for *Ostorhinchus doederleini*. No. of days = number

622 of days since fish were immersed in tetracycline.

623

| No. of days | <i>n</i> | SL range (mm) | Mean of counts (SE) |
|-------------|----------|---------------|---------------------|
| 5 | 42 | 17.0 - 25.2 | 4.95 (0.07) |
| 10 | 16 | 17.4 - 34.0 | 10.06 (0.11) |
| 15 | 11 | 16.2 - 25.0 | 14.82 (0.23) |

624

Table 3 Age (days) and size (mm; SL) of presettlement and recently settled *Ostorhinchus doederleini* in two recruitment seasons. Data shown are the mean (range) and total n is given by row. For recently settled fish n varied for size and age, more fish were collected for measurements of size and were not preserved in ethanol (Kingsford and Finn 1997).

| | 1994 | 1995 | <i>n</i> |
|-----------------------|------------------------|------------------------|----------|
| Presettlement fish | | | |
| SL | 10.7 (7.5 - 13.0) 4 | 10.6 (9.0 - 13.8) 30 | 34 |
| Age | 18 (15.7 - 19.7) 4 | 19.7 (16.0 - 26.0) 30 | 34 |
| Recently settled fish | | | |
| SL | 14.1 (9.8 - 18.0) 299 | 11.23 (8.6 - 18.0) 378 | 677 |
| Age | 28.2 (17.0 - 41.5) 113 | 22.5 (16.0 - 40.0) 119 | 232 |

631

632 **Table 4** von Bertalanffy growth parameters for four reefs and estimates of age maxima for individual
 633 fish from samples at each location and average age of the oldest five and 10 percent of fish (i.e. Max %).
 634

| Reef | n | L_{∞} | K | r^2 | Age Max | Max 5% (n) SE | Max10% (n) SE |
|-----------------|-----|--------------|-------|-------|---------|---------------|---------------|
| Heron | 122 | 76.24 | 0.008 | 0.86 | 215 | 173 (6) 13 | 144 (12) 11 |
| One Tree Island | 257 | 60.76 | 0.012 | 0.88 | 284 | 255 (13) 4 | 240 (26) 4 |
| Lamont | 91 | 83.84 | 0.006 | 0.82 | 368 | 213 (5) 6 | 176 (9) 27 |
| Fitzroy | 123 | 70.48 | 0.009 | 0.77 | 282 | 224 (6) 12 | 207 (12) 8 |
| All reefs | 593 | 65.04 | 0.010 | 0.89 | 368 | 249 (30) 5 | 226 (59) 4 |

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640 **Table 5** Size, age and sex differences for *Ostorhinus doederleini* collected at One Tree Island, October
641 2010.

| | Female | Male |
|------------|----------|----------|
| n | 55 | 70 |
| Mean (SL) | 53.27 mm | 52.09 mm |
| SE | 0.535 | 0.596 |
| Min (SL) | 43 mm | 41 mm |
| Max (SL) | 60 mm | 66 mm |
| Mean (Age) | 191 days | 190 days |
| Min (Age) | 139 days | 132 days |
| Max (Age) | 258 days | 263 days |

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Table 6 A comparison of with examples of demographic characteristics among multiple families of tropical reef fishes, by trophic groups (adapted from Randall et al. 1990); in some cases we found more references than listed, but the age range was within the other publication listed. A Yes (Y) indicates that some information is available; ND- no data, y- years, d- days. Brothers et al. (1983) provided estimates of PLD for many of the groups listed, but they relied on the presence of settlement marks which are not found in some families such as apogonids. Some families appear in more than one trophic group (e.g. Pomacentridae). Data from temperate regions are not included.

| Family | Species | Presettlement growth | PLD (range) | Settlement mark | Early Post-settlement growth | Life time growth | Age maxima | Estimates of mortality | Country | Source |
|--|---------------------------------------|----------------------|-------------|-----------------|------------------------------|------------------|------------|------------------------|------------------|---|
| Nocturnal planktivores/piscivores | | | | | | | | | | |
| Apogonidae | <i>Apogon cyanosoma</i> | N | 18-19d | ND | ND | ND | ND | ND | GBR, Australia | Brothers et al. 1983 |
| | <i>Cheilodipterus quinquelineatus</i> | N | 17-29d | ND | ND | ND | ND | ND | GBR, Australia | Brothers et al. 1983 |
| | <i>Ostorhinchus doederleini</i> | Y | 16-26d | ND | Y | Y | < 1 year | Y | GBR, Australia | This study |
| | <i>Ostorhinchus rubrimacula</i> | N | N | ND | Y | Y | < 1 year | ND | Fiji | Longenecker and Langston 2006 |
| Holocentridae | Multiple (7) | Y | 32-56d | ND | ND | ND | ND | ND | Western Atlantic | Tyler et al. 1993 |
| Pempheridae | | ND | ND | ND | ND | ND | ND | ND | | |
| Diurnal planktivores | | | | | | | | | | |
| Caesionidae | | ND | ND | ND | ND | ND | ND | ND | | |
| Pomacentridae | Multiple (8) | ND | 8-32d | Y | Y | ND | ND | ND | GBR, Australia | Bay et al. 2006; Green and McCormick 2005 |
| Acanthuridae | <i>Naso sp</i> (6) | ND | ND | ND | ND | Y | 9-30y | ND | GBR, Australia | Choat and Robertson 2002 |

| | | | | | | | | | | |
|----------------------------------|---|----|--------|----|----|----|---------|----|-------------------------------|--|
| Serranidae | e.g. <i>Anthias</i> spp. and <i>Pseudoanthias</i> spp | ND | ND | ND | ND | ND | ND | ND | | |
| Micro-Meso carnivores | | | | | | | | | | |
| Balistidae | Multiple (2) | ND | ND | ND | ND | Y | 11-14y | Y | Brazil | de Albuquerque et al. 2011; |
| Chaetodontidae | Multiple (8) | Y | 23-45d | Y | Y | Y | 6-20y | Y | GBR, Australia | Bernardes 2002 Fowler 1989; Berumen 2005; Berumen et al. 2012 |
| Gobiidae | Multiple (3) | ND | 24-26d | Y | Y | Y | 59-100d | Y | GBR, Australia | Depczynski and Bellwood 2006 |
| | <i>Coryphopterus kuna</i> | ND | 45-74d | Y | Y | Y | 120d | Y | Caribbean | Victor et al. 2010 |
| | <i>Eviota sigillata</i> | ND | 23-27d | Y | Y | Y | 59d | Y | GBR, Australia | Depczynski and Bellwood 2005 |
| Labridae | Multiple (9) | ND | 21-50d | Y | ND | Y | 15-36y | Y | GBR, Australia | Brothers et al. 1983; |
| | <i>Thalassoma bifasciatum</i> | Y | 40-72d | Y | Y | ND | ND | ND | Caribbean | Choat et al. 2006 Victor 1982 |
| Nemipteridae | <i>Scolopsis bilineatus</i> | ND | ND | ND | ND | Y | 16 | Y | GBR, Australia | Boaden and Kingsford 2012 |
| Pomacanthidae | <i>Pomacanthus imperator</i> | ND | ND | ND | ND | Y | 16 | ND | China | Chung and Woo 1999 |
| Macrocarvivore/ piscivore | | | | | | | | | | |
| Carangidae | Multiple (2) | ND | ND | ND | ND | Y | 6-10y | ND | Hawaii | Sudekum et al. 1991 |
| | <i>Caranx bucculentus</i> | ND | ND | ND | ND | Y | ND | Y | Northern Australia | Brewer et al. 1994 |
| Lethrinidae | Multiple (7) | ND | ND | ND | ND | Y | 15-36y | Y | GBR, Australia | Currey et al. 2013; Brown and Sumpton 1998 |
| Lutjanidae | Multiple (11) | ND | ND | ND | ND | Y | 12-55y | Y | Northern Australia, Indonesia | Marriott et al. 2007; Newman et al. 1996; Newman et al. 2000; Heupel et al. 2010 |
| | <i>Lutjanus carponotatus</i> | ND | ND | ND | ND | Y | 18y | Y | GBR, Australia | Kingsford 2009 |
| Scorpaenidae | <i>Pterois volitans</i> | ND | 20-35d | ND | ND | ND | ND | ND | Bahamas | Ahrenholz and Morris 2010 |
| Serranidae | <i>Cephalopholis cyanostigma</i> | ND | ND | ND | ND | Y | 45y | Y | GBR, Australia | Mosse et al. 2002 |
| | <i>Cromileptes altivelis</i> | ND | ND | ND | ND | Y | 19y | Y | GBR, Australia | Williams et al. 2009 |

| | | | | | | | | | |
|----------------------------------|----|----|----|----|---|-----|---|----------------|--------------------|
| <i>Epinephelus fuscoguttatus</i> | ND | ND | ND | ND | Y | 42y | Y | GBR, Australia | Pears et al. 2006 |
| <i>Plectropomus laevis</i> | ND | ND | ND | ND | Y | 16y | Y | GBR, Australia | Heupel et al. 2010 |
| <i>Plectropomus leopardus</i> | ND | ND | ND | ND | Y | 15y | Y | GBR, Australia | Kingsford 2009 |

| Omnivores/herbivores/ scrapers and detrital feeder | | | | | | | | | | |
|--|------------------------------------|----|--------|----|----|----|--------|----|-----------------------------------|---|
| Acanthuridae | Multiple (5) | ND | 84d | Y | ND | Y | 21-70y | ND | GBR, Australia | Choat and Axe 1996 |
| Blenniidae | Multiple (3) | ND | 12-33d | Y | ND | ND | ND | ND | GBR, Australia | Beldade et al. 2007; Brothers et al. 1983 |
| | <i>Salarias patzneri</i> | ND | ND | Y | Y | ND | 350d | ND | GBR, Australia | Wilson 2004 |
| Pomacentridae | Multiple (100) | Y | 12-39d | Y | ND | ND | ND | ND | GBR, Australia; Pacific, Atlantic | Bay et al. 2006; Wellington and Victor 1989 |
| | <i>Acanthochromis polyacanthus</i> | ND | ND | Y | Y | N | 9-11y | Y | GBR, Australia | Kingsford and Hughes 2005 |
| | <i>Pomacentrus amboinensis</i> | Y | 15-23d | ND | ND | ND | ND | ND | GBR, Australia | Kerrigan 1996 |
| | <i>Pomacentrus coelestis</i> | Y | 15-27d | Y | Y | ND | ND | ND | GBR, Australia | Kingsford et al. 2011 |
| | <i>Pomacentrus moluccensis</i> | ND | ND | ND | Y | Y | 18y | Y | GBR, Australia | Doherty and Fowler 1994 |
| | <i>Stegastes acapulcoensis</i> | ND | ND | ND | ND | Y | 12-32y | Y | Panama, Galapagos | Meekan et al. 2001 |
| Scaridae | Multiple (7) | Y | 30-50d | Y | ND | Y | 5-20y | Y | GBR, Australia | Brothers et al. 1983; Gust et al. 2002; Choat et al. 1996 |
| | <i>Sparisoma viride</i> | ND | ND | ND | ND | Y | 7-9y | Y | Caribbean | Choat et al. 2003 |

644

645

Figure Captions

Fig. 1 Map showing the location of the four reefs in the Capricorn-Bunker Group, southern Great Barrier Reef, Australia where *Ostorhinchus doederleini* was collected.

Fig. 2 (a) Sagittal otolith section of a 21 day old *Ostorhinchus doederleini*. Width of otolith section is 1500 μm . Initial measurement made at first visible increment (Insert showing enlargement of 300 μm long); (b) Otolith of a fish euthanised 10 days after immersion in tetracycline viewed under UV light, scale bar = 100 μm ; (c) A section of an 90 day old fish (from OTI; 34 mm SL) showing track used for aging, which extended from the primordium to the outer edge of the otolith along the longest axis (Section is 2100 μm long).

Fig. 3 Otolith increment widths plotted as a function of increment number for a subset of four post-settlement *Ostorhinchus doederleini*, (a) 1994 and 1995; (b) 2010 from One Tree Island, Great Barrier Reef, Australia. The dotted vertical line indicates the mean no. of increments deposited by presettlement apogonids caught just prior to settlement measured from the primordium to along the sulcal groove; from the primordium to the ventral edge of the otolith. Initial measurement made at first visible increment.

Fig. 4 Relationship between standard length and age (days) of presettlement versus newly settled recruits *Ostorhinchus doederleini* in 1994 and 1995 together with fitted regression lines and summary statistics.

Fig. 5 von Bertalanffy growth curves for *Ostorhinchus doederleini* for the four reefs in the Capricorn Bunker group, Great Barrier Reef, Australia.

Fig 6 Age-based ‘catch-curves’ that provide estimates of mortality for *Ostorhinchus doederleini* for Heron and Lamont reefs in the Capricorn Bunker group, Great Barrier Reef, Australia; each data point indicates Log_e frequency of each age class.

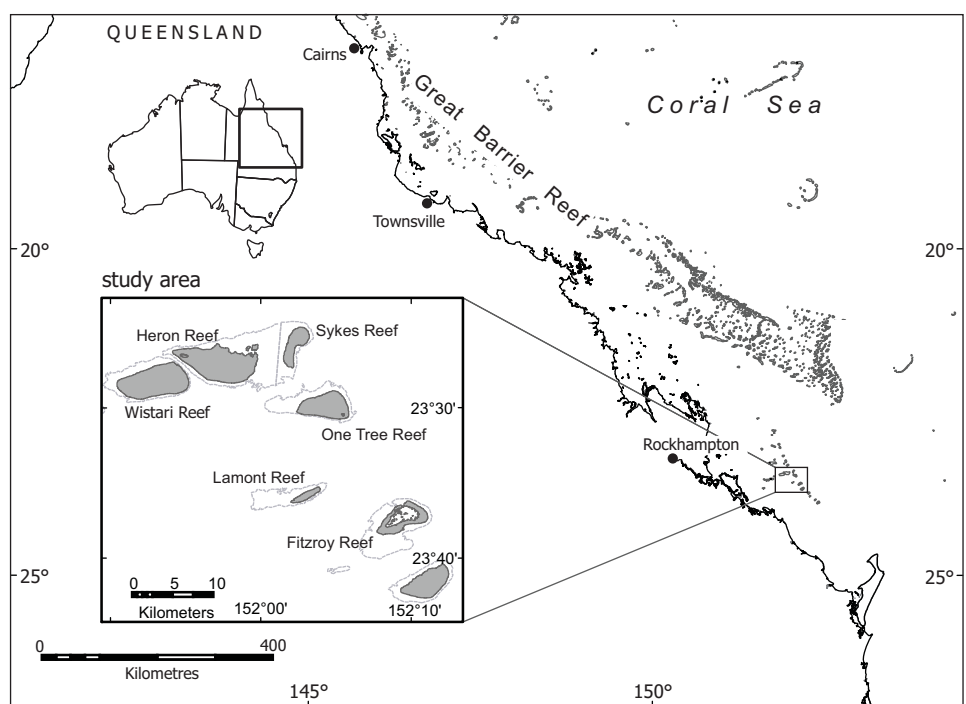


Figure 2

